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A review of the nematode tribe Macropostrongylinea Lichtenfels, 1980 (Strongyloidea, Cloacininae) from Australian marsupials with the erection of a new tribe, Coronostrongylinea

by Ian Beveridge

Abstract. — The composition of the nematode tribe Macropostrongylinea Lichtenfels, 1980, is reviewed and the morphological characters of the various genera discussed. The Macropostrongylinea is characterised by a poorly sclerotised buccal capsule supported externally by sets of muscle bands passing from the buccal capsule wall to the somatic musculature, by an elongate oesophagus with a claviform bulb and generally an enlargement of the anterior end of the intestine. Genera admitted are *Alocostoma* Mawson, 1979, *Foliostoma* Beveridge & Johnson, 1981, *Macroponema* Mawson, 1978, *Macropostrongylus* Yorke & Maplestone, 1926, *Monilonema* Beveridge & Johnson, 1981, and *Trigonostonema* Beveridge, 1981. *Cassunema* Beveridge & Johnson, 1981, is transferred to the Zoniolaiminea (Popova, 1952). A new tribe, Coronostrongylinea, is created for the genera *Coronostrongylus* Johnston & Mawson, 1939, *Papillostrongylus* Johnston & Mawson, 1939, *Popovastrongylus* Mawson, 1977, and *Thylonema* Beveridge, 1981, characterised by a buccal capsule formed of two different longitudinal layers, the inner layer transparent and the outer layer sclerotised and frequently reduced to an annulus.

Résumé. — Les genres appartenant à la tribu Macropostrongylinea Lichtenfels, 1980, sont examinés et leurs caractères morphologiques sont discutés. La tribu Macropostrongylinea est caractérisée par une capsule buccale non sclérotisée avec plusieurs bandes de muscles entre l'extérieur de la capsule et les muscles somatiques, et par un œsophage long avec un bulbe claviforme et un élargissement de l'extrémité antérieure de l'intestin. Les genres admis dans la tribu sont les suivants : *Alocostoma* Mawson, 1979, *Foliostoma* Beveridge & Johnson, 1981, *Macroponema* Mawson, 1978, *Macropostrongylus* Yorke & Maplestone, 1926, *Monilonema* Beveridge & Johnson, 1981, and *Trigonostonema* Beveridge, 1981. *Cassunema* Beveridge & Johnson, 1981, est transféré dans la tribu Zoniolaiminea (Popova, 1952). Une tribu nouvelle, Coronostrongylinea, est créée pour les genres *Coronostrongylus* Johnston & Mawson, 1939, *Papillostrongylus* Johnston & Mawson, 1939, *Popovastrongylus* Mawson, 1977, et *Thylonema* Beveridge, 1981 ; elle est caractérisée par une capsule buccale formée de deux parties : une partie interne transparente et une partie extérieure sclérotisée, souvent remplacée par un anneau.

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The nematode tribe Macropostrongylinea was created by Lichtenfels (1980) to contain a number of genera within the Cloacininae Stossich, 1899, parasitic in the stomach of Australian macropodid marsupials, and characterised by a poorly sclerotised buccal capsule

sometimes supported by a ring-like thickening and lacking a corona radiata. The tribe initially contained the genera *Coronostrongylus* Johnston & Mawson, 1939, *Macroponema* Mawson, 1978, *Macropostrongylus* Yorke & Maplestone, 1926, *Papillostrongylus* Johnston & Mawson, 1939, and *Popovastrongylus* Mawson, 1977. Subsequently *Alocostoma* Mawson, 1979, was added to the tribe (BEVERIDGE, 1981*a*) along with the new genera *Trigonostonema* Beveridge, 1981, *Thylonema* Beveridge, 1981, *Cassunema* Beveridge & Johnson, 1981, *Foliostoma* Beveridge & Johnson, 1981, and *Macroponema* Beveridge & Johnson, 1981. BEVERIDGE and JOHNSON (1981) modified the definition of the tribe given by LICHTENFELS (1980) but retained the poorly sclerotised buccal capsule as the principal distinguishing feature of the tribe and provided a key to the genera.

Additional species belonging to these genera were described by BEVERIDGE (1985 ; 1986*a*, *b*, *c*) providing new information on the morphological characteristics of certain genera and a clearer definition of the features of the buccal capsule. In this paper, the relationships of the genera are re-assessed in the light of the new morphological evidence available. In order to provide comparable and complete descriptions of the cephalic morphology of all the genera involved, redescriptions are given of the heads of species of *Papillostrongylus* and *Macroponema*.

Papillostrongylus labiatus Johnston & Mawson, 1939

(Fig. 1)

MATERIAL EXAMINED : 2 ♀, from stomach, *Macropus dorsalis* (Gray, 1837), Milman, Queensland, Australia, 5.VII.1982, coll. I. BEVERIDGE.

DESCRIPTION

Mouth opening dorso-ventrally elongate ; amphids on prominent conical projections on either side of mouth opening ; submedian papillae conical, each bearing a single small seta ; prominent beak-like, triangular projection present on dorsal and ventral aspects of mouth opening ; leaf crowns absent. Buccal capsule with heavily sclerotised outer wall, walls sinuous, thicker posteriorly ; inner part of buccal capsule wall thick, transparent, variously folded in lower part of buccal capsule ; buccal capsule dorso-ventrally elongate at anterior end, becoming circular in cross section posteriorly ; buccal capsule not supported externally by set of muscles.

DISCUSSION

The presence of a buccal capsule with a heavily sclerotised outer wall and with a transparent internal lining aligns the genus *Papillostrongylus* with *Coronostrongylus, Popovastrongylus* and *Thylonema*. It differs from all of these genera in the lateral flattening of the anterior end of the buccal capsule and in the presence of beak-like dorsal and ventral projections arising around the mouth opening. The species was initially described from *Macropus dorsalis* from Queensland, and the material described above came from the same host species and the same geographic region. MAWSON (1964) redescribed the species from

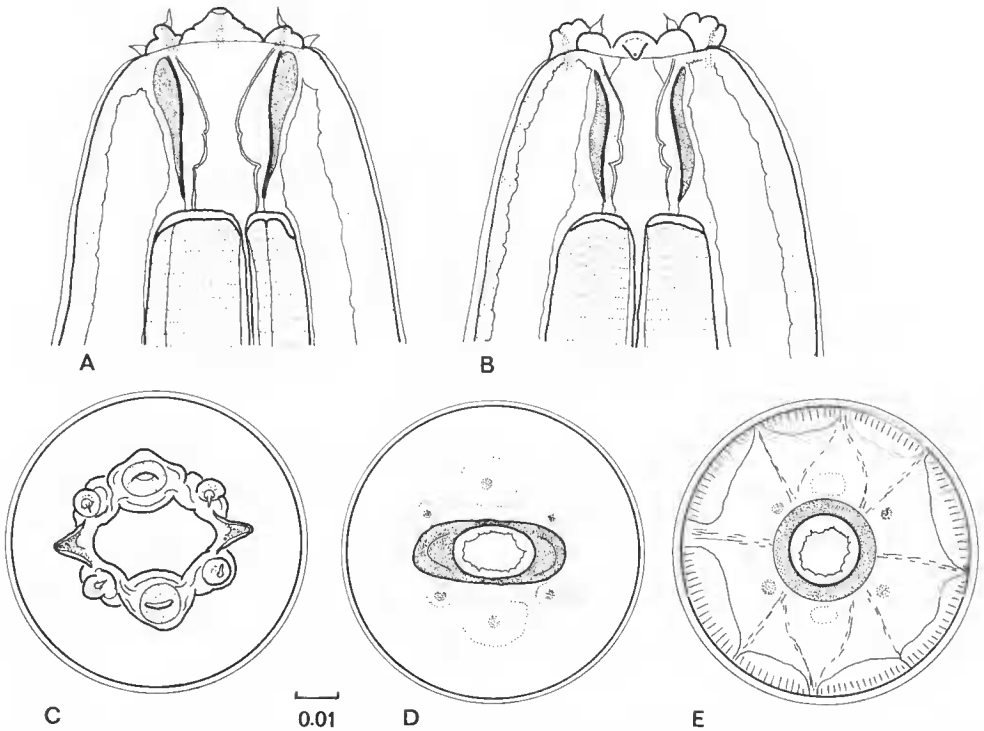

FIG. 1. — *Papillostrongylus labiatus* Johnston & Mawson, 1939 : A, head, lateral view ; B, head, dorsal view ; C, mouth opening, apical view ; D, optical transverse section through anterior extremity of buccal capsule ; E, optical transverse section through mid-region of buccal capsule. (Scale line 0.01 mm.)

Macropus giganteus Shaw, 1790 (= *M. canguru*) and from *M. rufus* (Desmarest, 1822) and the general morphological features given in her redescription conform to those given above. However, she noted paired setae on the cephalic papillae and a tiny leaf crown, neither of which could she find on re-examining the type specimens. The description given above confirms her observations since a leaf crown and paired setae are definitely absent in specimens from *M. dorsalis*, suggests that in fact two species are currently included under the name *labiatus* and that the material described by MAWSON (1964) in fact belongs to an undescribed species.

Macroponema comani Mawson, 1978

(Fig. 2)

MATERIAL EXAMINED : 11 ♂, 32 ♀, from stomach, *Macropus robustus* Gould, 1841, Pallamana Station via Charters Towers, Queensland, Australia, 28.III.1983, coll. R. SPEARE. Specimens in the Australian Helminthological Collection, Adelaide, no. 13146, and Muséum national d'Histoire naturelle, Paris, no. 525HD.

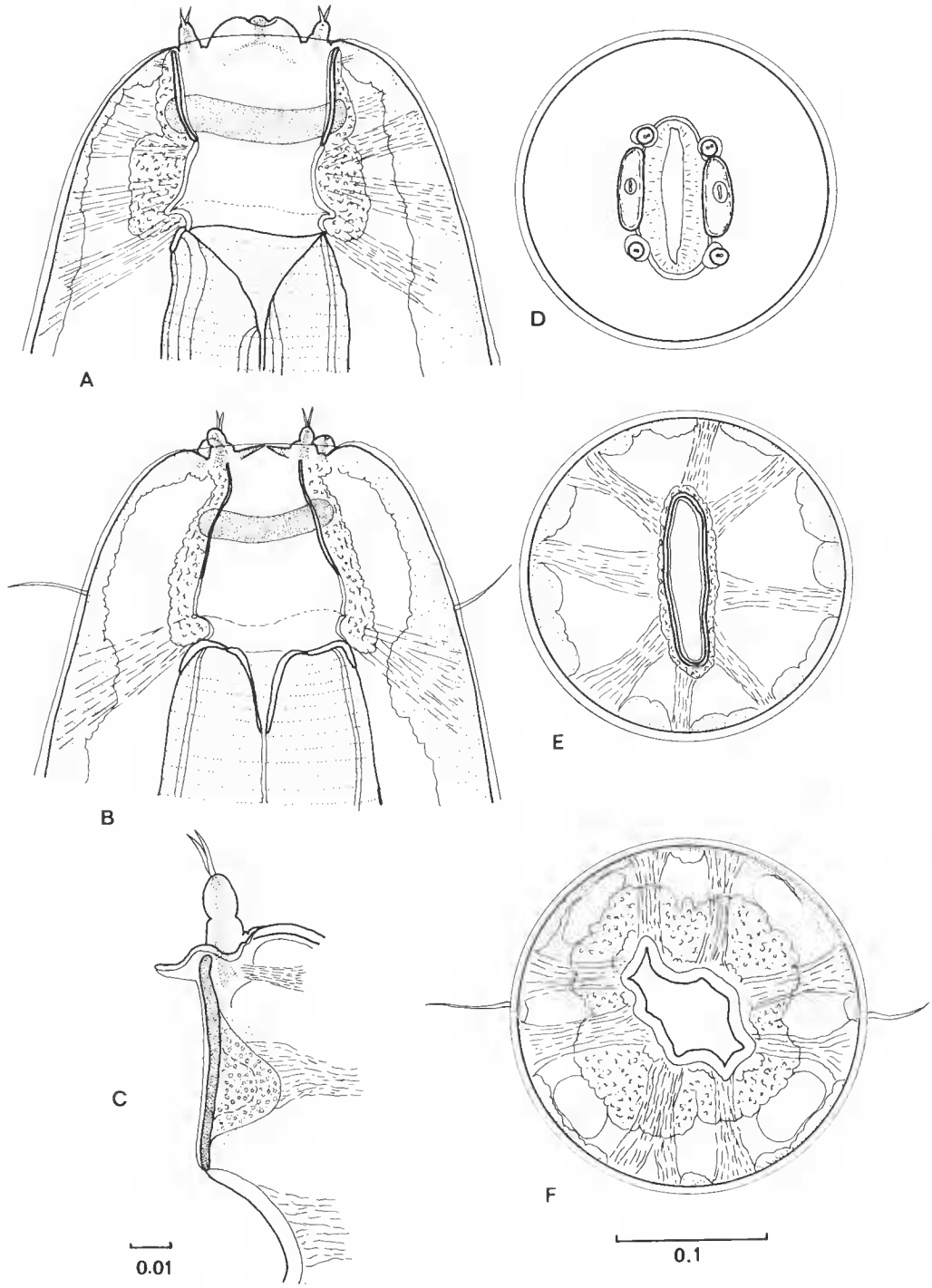

FIG. 2. — *Macroponema comani* Mawson, 1978 : A, head, lateral view ; B, head, dorsal view ; C, optical longitudinal section through anterior part of buccal capsule, showing muscles and labial structures ; D, mouth opening, apical view ; E, optical transverse section through anterior region of buccal capsule ; F, optical transverse section through posterior part of buccal capsule, at level of deirids. (Scale lines in mm.)

Description

Mouth opening dorso-ventrally elongate, narrow, capable of being completely closed ; cephalic collar absent ; amphids borne on dorso-ventrally elongate projections of peri-oral cuticle on either side of mouth opening ; submedian papillae conical, almost jointed, situated dorsal and ventral to projections bearing amphids, each armed with 2 prominent setae ; peri-oral cuticle extends into mouth opening to form 2 striated, elongate flanges, extending along either side of the mouth opening and corresponding to a labial crown in related genera. Buccal capsule composed of two sections ; anterior section with relatively thick and moderately rigid outer wall with narrow, transparent lining ; posterior section with thick, non retractile but pliable outer wall ; anterior part of buccal capsule supported externally by annulus of non retractile material ; anterior part of buccal capsule flattened laterally, supported externally by set of 8 muscle bands running from annulus to somatic musculature ; small duplicate set of muscles attaches to outer wall of buccal capsule near anterior extremity, visible only in dissections of head ; posterior part of buccal capsule surrounded externally by ill-defined mass of opaque tissue ; 2 sets each of 8 muscle bands pierce surrounding tissues to attach to external surface of buccal capsule ; buccal capsule eight sided in transverse section but laterally compressed ; additional set of 8 muscle bands attach at junction of oesophagus with buccal capsule.

Discussion

Macroponema comani possesses the most complex buccal capsule of the various genera of the Macropostrongylinea. The division of the buccal capsule into distinct anterior and posterior regions and the presence of a total of five sets of muscle bundles supporting the buccal capsule shows a degree of complexity of organisation not met with previously in the tribe. Several of the sets of muscles were only visible in dissections of the head, and can be readily overlooked in examining entire specimens. The lateral compression of the buccal capsule and mouth opening readily distinguishes *Macroponema* from all other genera of the tribe with non sclerotised buccal capsules.

M. comani occurs commonly in *Macropus giganteus* (Mawson, 1978 ; Beveridge & Arundel, 1979). It is reported for the first time from *Macropus robustus*.

Morphological features of the Macropostrongylinea

1. The buccal capsule

All genera of the Macropostrongylinea are characterised by a buccal capsule more or less composed of two longitudinal layers. The inner layer is transparent, frequently very thick and may be folded longitudinally (*Coronostrongylus, Alocostoma*), may form a shelf in the buccal capsule (*Popovastrongylus pearsoni, P. wallabiae*) or may be so inflated as to almost occlude the lumen of the buccal capsule (*Popovastrongylus macropodis*). The same

internal lining of the buccal capsule is continuous externally with the peri-oral cuticle and may be variously modified into prominent lobes (*Macropostrongylus*), a labial crown of few elements (*Monilonema*), or a crown of numerous tiny elements (*Trigonostonema*).

The form of the outer part of the buccal capsule conveniently divides the tribe into two groups of genera depending upon whether or not it is sclerotised. In the first group of genera, the outer part of the wall is highly retractile, apparently rigid and may extend as a cylinder with sinuous margins (*Papillostrongylus, Popovastrongylus*) or may be reduced to a sclerotised annulus in the mid-region of the buccal capsule (*Coronostrongylus, Thylonema*). Species such as *Popovastrongylus thylogale* are intermediate to the extent that there is a distinct annulus but thin cylindrical buccal capsule walls remain. In the second group of genera, the outer part of the buccal capsule is non sclerotised, non retractile, apparently pliable in shape and its shape is maintained by sets of muscle bands which extend from the outer wall of the buccal capsule to the somatic musculature. An annulus or other thickening of the buccal capsule wall is frequently present, and if present, one of the sets of muscles inserts onto it. Contraction of the muscles opens the buccal capsule and closure is presumably effected by the pressure of the fluid in the peri-enteric cavity when the muscles relax. The genera with a non sclerotised buccal capsule and supporting muscles are : *Alocostoma, Foliostoma, Macroponema, Macropostrongylus, Monilonema* and *Trigonostonema.*

The phylogenetic relationships between the two groups of genera are indicated by the morphology of the buccal capsule of the larval stages in species of *Macropostrongylus*. In both *M. macrostoma* and *M. yorkei*, the fourth larval stage possesses a sclerotised outer wall to the buccal capsule with a simple, unmodified, transparent inner lining. Muscles supporting the buccal capsule are absent, but there is a set of muscles attaching the anterior end of the oesophagus to the somatic muscles. In the adults of these two species, the sclerotised buccal capsule is replaced by a non sclerotised one and the external muscles appear (Beveridge, 1985). For this reason, the two groups of genera within the tribe are considered to be related ; sclerotised buccal capsules are considered plesiomorphic and non sclerotised buccal capsules apomorphic. The fourth stage larvae of *Macropostrongylus* spp. most closely resemble adults of *Popovastrongylus* in features of the buccal capsule, and for this reason *Popovastrongylus* is postulated as a likely ancestor for the genera with non sclerotised buccal capsules.

2. Buccal capsule symmetry

Genera of the Macropostrongylinea show considerable plasticity in the shape of the buccal capsule compared with other tribes of the Cloacininae (see Beveridge and Johnson, 1981). In all other tribes, the buccal capsule is circular in cross section, and it is therefore assumed that this shape is plesiomorphic within the Macropostrongylinea. Among the genera with sclerotised buccal capsules, capsules which are circular in transverse section are found in the genera *Coronostrongylus* and *Popovastrongylus* (except *P. thylogale*). In the genus *Thylonema*, the buccal capsule is dorso-ventrally flattened (Beveridge, 1981*b*), while in *Papillostrongylus*, the anterior part of the buccal capsule is laterally flattened, but becomes circular in the posterior part. In *Popovastrongylus thylogale* the buccal capsule and mouth opening are approximately triangular in shape with the base of the triangle dor-

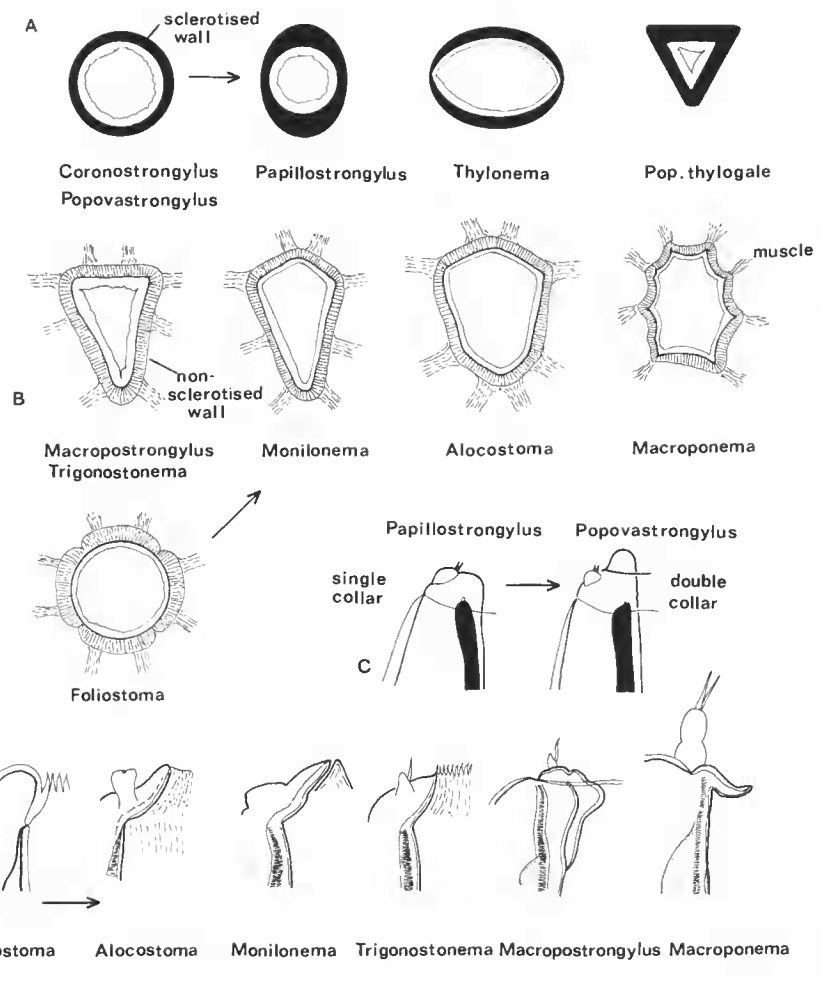

FIG. 3. — A, B, transverse sections of buccal capsules of genera of the Macropostrongylinea ; C, optical sections through mouth openings of *Papillostrongylus* and *Popovastrongylus* showing, schematically, arrangement of cephalic and labial (stippled) collars ; D, optical sections through mouth openings and buccal capsules of genera with non sclerotised buccal capsules showing different morphological features of the labial region.

sal, that is with a symmetry comparable with the oesophagus. In *P. macropodis* the sclerotised wall of the buccal capsule is circular in section, but the inflated lining has a triradiate symmetry similar to that of the oesophagus.

Within the group of genera lacking a sclerotised buccal capsule, the shape of the buccal capsule is determined in part by the supporting musculature. A radially symmetrical buccal capsule is present in *Foliostoma*, however, in *Alocostoma, Macropostrongylus, Monilonema* and *Trigonostonema*, the buccal capsule is either triangular in section with the base of the triangle dorsal (*Macropostrongylus, Trigonostonema*) or slightly modified so as to form a

quadrilateral (*Monilonema*) a pentagon or a hexagon (*Alocostoma*). Slight variations do occur within genera, but all the patterns described (BEVERIDGE, 1985 ; 1986*a*, *c*) are considered as modifications of a basic triangular structure.

In *Macroponema comani*, the structure of the posterior part of the buccal capsule is eight sided, but it is dorso-ventrally flattened. By contrast, the anterior part of the buccal capsule which has a more feeble set of supporting muscles, is markedly compressed dorso-ventrally and in effect has only dorsal and ventral sides. Because of the marked dorso-ventral compression of the entire buccal capsule in this species, the genus *Macroponema* is considered distinct from the group of genera with triangular buccal capsules.

In both groups of genera, the buccal capsule which is circular in transverse section is considered plesiomorphic, and the various non circular shapes apomorphic.

3. Labial structures

A distinct cephalic collar separates the labial structures from the remainder of the body in *Coronostrongylus, Popovastrongylus, Papillostrongylus* and *Thylonema*. The collar is simple in *Coronostrongylus* with the cephalic papillae projecting from it. Because the same simple form of collar occurs in the Cloacininea (STOSSICH, 1899) and in primitive members of the Zoniolaiminea (POPOVA, 1952), it is also considered plesiomorphic for the Macropostrongylinea. In *Papillostrongylus*, a simple collar is present, but the cephalic papillae are modified and extra labial appendages are developed. By contrast, in *Popovastrongylus* the collar is double, with the appearance of an extra, internal labial collar which is sometimes ornamented. The structure is analogous to the internal collar present in *Rugopharynx* Mönnig, 1927, and was described in detail by BEVERIDGE (1982). The same terminology has therefore been applied to the oral structures in *Popovastrongylus*. They are considered to be derived characters and to have developed in parallel in the Pharyngostrongylinea Popova, 1952.

In the genera of the Macropostrongylinea with non sclerotised buccal capsules, modifications of the labial region are present which are clearly related. In *Alocostoma*, a simple, continuous medially-directed lobe of tissue overhangs the mouth opening, reducing the size of the opening. As it resembles the internal collar present in *Popovastrongylus*, it has been termed a labial collar (BEVERIDGE, 1986*c*). In the species of *Monilonema*, the analogous structure is subdivided into eight or twenty regular elements resembling a leaf crown. The structure was described as a "leaf crown-like flange" in *M. lacunosa* (BEVERIDGE & JOHNSON, 1981), but since it is clearly a labial structure, it is here designated a labial crown, following the terminology of BEVERIDGE (1982) for the Pharyngostrongylinea. The anterior part of the buccal capsule and the labial region of species of *Macropostrongylus* are developed into eight lobes, providing the genus with its principal differentiating character. The labial projections around the mouth opening in *Trigonostonema*, have on their free edge a crown of numerous tiny irregular elements giving the lips a frayed appearance, while in *Foliostoma*, the same type of structure occurs around the anterior extremity of the buccal capsule, but there are no overhanging lobes of labial tissue. The characters in *Foliostoma* (lack of labial development, crown at opening of buccal capsule) are considered to be plesiomorphic, with the various labial developments being considered apomorphic. This development parallels precisely the developments in the symmetry of the buccal capsule.

A shelf-like labial extension is present at the mouth opening of *Macroponema comani* and is analogous to the labial crown of *Monilonema*, but is not subdivided into numerous elements. Because of the general dorso-ventral elongation of the mouth opening in *Macroponema*, the labial structures form two elongate projections along either side of the mouth opening. The development of labial structures within the Macropostrongylinea with non sclerotised buccal capsules has therefore also occurred in parallel with the Pharyngostrongylinea.

4. Intestine and oesophagus

In *Macropostrongylus, Monilonema* (one species), *Alocostoma* and *Trigonostonema* the anterior part of the intestine is modified into paired dilatations which partially enclose the oesophageal bulb. They are poorly developed in the fourth stage larvae of *Macropostrongylus* and are absent in *Coronostrongylus, Papillostrongylus* and *Popovastrongylus*. The dilatations are considered derived characters and their presence or absence generally parallels the evolutionary trends in the buccal capsule. A parallel development has occurred in the Pharyngostrongylinea.

The oesophagus of *Popovastrongylus* and *Coronostrongylus* terminates in a spherical bulb. This character is considered plesiomorphic since it occurs in primitive genera of the Zoniolaiminea. It is replaced in the genera with non sclerotised buccal capsules by an elongate clavate bulb, and the oesophageal corpus is frequently elongate and may even be subdivided into distinct regions. The latter characters are thought to be apomorphic.

5. Amphids

In several genera of the Macropostrongylinea, the amphids are borne on prominent conical projections. Although a minor morphological character, it occurs only within the Macropostrongylinea. The character is absent in *Alocostoma, Coronostrongylus, Trigonostonema* and in *Thylonema.*

Relationships of genera

The structure of the buccal capsule of genera of the Macropostrongylinea clearly separates this tribe from the remaining tribes of the Cloacininae. In no other tribe is the buccal capsule divided into an internal transparent part and an external sclerotised part, or has the external part of the buccal capsule wall replaced by a pliable, non sclerotised structure with external supporting muscles. The same character divides the Macropostrongylinea into two distinct groups of genera, and the division is supported to some extent by the structure of the oesophagus and the thickening of the anterior part of the intestine. The relationship between these two related group of genera is clearly indicated by the development of the buccal capsule in species of *Macropostrongylus* (Beveridge, 1985) which shows that the sclerotised buccal capsule is a plesiomorphic character, and that the genera with non sclerotised buccal capsules may have evolved from genera ancestral to *Popovastrongylus*. Within each of these two groups of genera, development of the buccal capsule struc-

tures has followed a similar course, with buccal capsules which are initially circular in transverse section becoming either laterally or dorso-ventrally flattened, or becoming triangular in shape. Similarly, the labial region has become more complex in both group of genera with the development of labial collars in the *Coronostrongylus — Popovastrongylus* lineage, and the development of labial crowns and labial collars in the lineage with non sclerotised buccal capsules. These developments have a close parallel in the Pharyngostrongylinea which has been described by BEVERIDGE (1982).

The genus *Cassunema* has not been included in the Macropostrongylinea since its buccal capsule does not conform to any of the forms described above which are now considered characteristic for the tribe. Re-examination of type and other material has shown that although the buccal capsule is not heavily sclerotised, the external muscle system is lacking, and it therefore fits into neither of the groups of genera described above. BEVERIDGE & JOHNSON (1981) noted that in this species the oesophagus was greatly elongated with a spherical bulb lined by sclerotised plates, typical of the genera *Zoniolaimus* Cobb, 1898, and *Wallabinema* Beveridge, 1983, both of which belong to the Zoniolaiminea. The other character of the genus was the presence of striations in the lining of the buccal capsule around the mouth opening. In some of the new material examined, the structures are detached at their anterior extremities giving the appearance of a vestigial external leaf crown. An external leaf crown occurs in the genus *Tethystrongylus* Beveridge, 1983, which has an oesophagus similar to that of *Cassunema*. Because of these similarities, *Cassunema* is transferred to the Zoniolaiminea, and aligned with *Tethystrongylus*.

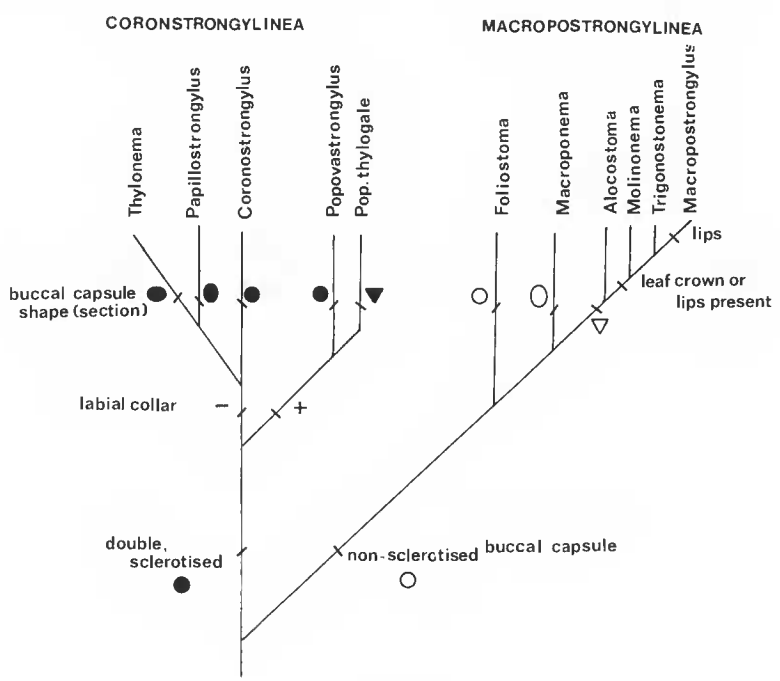

FIG. 4.

The Macropostrongylinea is here divided into two distinct tribes. The genera with non sclerotised buccal capsules supported externally by sets of muscles are retained within the Macropostrongylinea, while a new tribe, Coronostrongylinea trib. nov. is proposed for the genera with sclerotised outer buccal capsule walls with the name being chosen from what is thought to be the most primitive genus within the new tribe. Definitions of the two tribes are given below. Relationships between the genera are indicated schematically in figure 4.

Tribe MACROPOSTRONGYLINEA Lichtenfels, 1980

Small nematodes without alae. Mouth opening round or triangular in shape, with either labial collar, labial crown, lobed labial region or external leaf crown. Buccal capsule poorly sclerotised with thin transparent lining, supported externally by sets of muscle bands usually in eights, extending from external surface of buccal capsule to somatic musculature. Buccal capsule either circular, triangular or dorso-ventrally flattened in transverse section. Oesophagus elongate, bulb elongate, clavate, not lined with sclerotised plates ; anterior extremity of intestine enlarged. Dorsal ray of bursa with 2 pairs of branches. Spicules elongate, alate. Vulva immediately anterior to anus. Vestibule oriented longitudinally or transversely, prodelphic. Egg ellipsoidal. Parasitic in stomachs of macropodid marsupials.

Genera : *Alocostoma* Mawson, 1979, *Foliostoma* Beveridge & Johnson, 1981, *Macroponema* Mawson, 1978, *Macropostrongylus* Yorke & Maplestone, 1926, *Monilonema* Beveridge & Johnson, 1981, *Trigonostonema* Beveridge, 1981.

Tribe CORONOSTRONGYLINEA trib. nov.

Small nematodes without alae. Mouth opening round, triangular or oval, without lips or teeth ; labial collar present or absent. Buccal capsule formed of two distinct layers ; inner layer thick, transparent, occasionally folded ; outer layer sclerotised, cylindrical or reduced to an annulus ; supporting musculature absent. Buccal capsule circular triangular or oval in transverse section. Oesophagus with elongate corpus, not subdivided ; oesophageal bulb spherical without sclerotised plates, sometimes claviform ; anterior extremity of intestine not modified. Dorsal ray of bursa with 2 pairs of branches. Spicules elongate, alate. Vulva immediately anterior to anus. Vestibule oriented longitudinally, rarely obliquely, prodelphic. Egg ellipsoidal. Parasitic in stomachs of macropodid marsupials.

Genera : *Coronostrongylus* Johnston & Mawson, 1939, *Papillostrongylus* Johnston & Mawson, 1939, *Popovastrongylus* Mawson, 1977, *Thylonema* Beveridge, 1981.

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